

THE GENUS *LAGENA* (STRAMENOPILA: OOMYCOTA), TAXONOMIC HISTORY AND NOMENCLATURE

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ABSTRACT

A significant and morphologically distinct plant parasite, affecting roots of cultivated wheat and related grasses, *Lagena* has received little taxonomic attention. This genus, of oomycete affinity, has proved difficult to place with certainty in any particular oomycete group, especially in the absence of molecular sequence data. The generic nomenclature of *Lagena* was also uncertain, given a proposed replacement name, *Lagenocystis*, which I argue represents an unnecessary nomenclatural change. Several taxa (or potential taxa) have been, directly or indirectly, suggested for inclusion in *Lagena*. However, available evidence suggests retention of *Lagena* as monotypic, the only certain species being *L. radiculicola*. *Phytologia* 93(2): 157-167 (August 1, 2011)

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Vanterpool and Ledingham (1930) described the genus *Lagena* for a “phycomycete” (oomycete) parasite found in wheat, rye and barley roots in fields in Saskatchewan. A single species, *L. radiculicola*, was included in this genus. One to several thalli may occur in individual host cells, such as root-hair or cortical cells. The simple, sac-like thallus (Fig. 1) usually remains connected to the host cell by a persistent neck and “collar” (determined by Barr and Désaulniers, 1990, to be contributed by host callus material in response to penetration by the parasite). The thallus becomes multinucleate, and is holocarpic, yielding infective zoospores (Figs. 1, 5, 7) formed in an external vesicle at the tip of a discharge tube (Figs. 3, 4). Empty sporangia may be evident (Fig. 6), still exhibiting the neck region and discharge tube. Undifferentiated gametangia (resembling sporangia), bridged by

conjugation tubes, were described in (apparently isogamous) sexual reproduction leading to oospore formation (Figs. 8-10), cf. Vanterpool and Ledingham (1930). Additional observations by Truscott (1933), in Ontario, and Macfarlane (1970), in Europe, further established morphological variation of this unique organism. Truscott noted that the thallus (sporangium) may be branched (Fig. 2). Macfarlane observed that the thallus could assume a more elongate, tubular form, perhaps becoming twisted, but still not growing from one host cell to another. Photographs of oospores (resting spores) of *L. radiculicola* by Macfarlane (1970) show that these can be eccentric [a term related to the position of the reserve food globule in the oospore, cf. Dick, 1969] compared to the centric spores illustrated by Vanterpool and Ledingham (1930)—cf. Figs. 11, 12. Vanterpool and Ledingham illustrated development of a single oospore in a female gametangium; however, Truscott (1933) thought several oospores might develop in one such structure. The occasional abundance of *Lagena radiculicola*, its association with species of *Pythium* in “browning root rot” of cereals, and infection of related wild grasses (e.g., *Agropyron repens*) were also observed. Host symptoms involved the stunting, tip-crooking, and necrosis of small infected lateral roots. *Lagena* was included by Sprague (1950) in *Diseases of Cereals and Grasses in North America*.

SYSTEMATIC RELATIONSHIPS

The possible taxonomic relationship of *Lagena* with *Lagenidium* and *Pythium* was suggested by Vanterpool and Ledingham (1930), a conclusion generally supported by others (Fitzpatrick, 1930; Bessey, 1950; Macfarlane, 1970). Sparrow (1939) noted resemblance of *Lagena* to single-celled species of *Lagenidium* infecting algae or rotifer eggs; see also Seymour and Johnson (1973). Sparrow (1960) placed *Lagena* in the Lagenidiaceae, dealing at the time only cursorily with the genus since it is not aquatic. Karling (1981) noted that Vanterpool and Ledingham (1930) considered *Lagena* to possibly represent a link between the Lagenidiaceae and Pythiaceae. Karling (1981) believed *Lagena* to have characteristics in common with *Lagenidium* and *Myzocyttium* (another genus in the Lagenidiaceae), and with *Pythium*.

The systematic position of *Lagena* continued to be uncertain. Dick (1971) thought that oospore structure of *Lagena* (“*Lagenocystis*”)

was similar to certain oospores of the Saprolegniaceae (see Dick, 1969, re: oomycete oospores). Seymour and Johnson (1973), however, believed that some characteristics of *Lagen* oospores were suggestive of oospores of the Leptomitaceae (a family related to the Saprolegniaceae). Seymour and Johnson (1973) also mentioned the potential relationship of an unnamed (*Lagenidium*-like) rotifer parasite they described—and, by associative discussion, of *Lagen* *radicicola*—to *Myzocyttium*, a genus distinguished from *Lagenidium* by comparatively undifferentiated sexual structures. In contrast to *Lagen* (and *Lagenidium*), gametangial copulation in *Myzocyttium* is said to often be poroidal, i.e., not necessarily involving obvious fertilization tubes (cf. Canter, 1947; Karling, 1981). Although male and female gametangia of *Myzocyttium* are often more similar than in *Lagenidium*, they are often more readily distinguished than in *Lagen*. Barr and Désaulniers (1990) illustrated variation in number and shape of resting spores (oospores) of *L. radicicola* consistent with collective observations of earlier investigators (Vanterpool and Ledingham, 1930; Truscott, 1933; Macfarlane, 1970). Barr and Désaulniers (1990) posited a general lagenidialean affinity for *Lagen*, not inconsistent with views, for example, of Vanterpool and Ledingham (1930) and Sparrow (1960).

The zoospore of *Lagen* *radicicola* has been discussed as laterally biflagellate (cf. Karling, 1981) and subapically biflagellate (cf. Barr and Désaulniers, 1987). Although apparently variable in this regard (cf. Dick, 2001), these zoospores (Figs. 5, 7) are always biflagellate, and the two flagella (often oriented in at least somewhat different directions) are never truly apical—features suggestive of general stramenopilous affinity. Barr and Désaulniers (1987) described the structure and ultrastructure of the *Lagen* zoospore as indicating probable relationship to Oomycetes; however, they could not pin down this connection further, since the zoospore of *Lagen* lacks the concertina-like helix structure in the flagellar transition zone, characteristic of most oomycete zoospores. A transitional helix, if often simpler in form, is a feature of zoospores of various heterokonts. As noted by Barr and Désaulniers (1987), the *Lagen* zoospore was similar in the absence of a transitional helix to zoospores of the Phaeophyceae. Zoospores of *Lagen* also lack K-bodies or comparable structures (Barr and Désaulniers, 1987), features useful as phylogenetic markers (Powell et al., 1985; Beakes, 1989). The absence of K-body (or similar)

vesicles in the *Lagen* zoospore is not supportive of a close relationship with members of the Saprolegniaceae and Leptomitaceae (cf. paragraph above), the zoospores of which typically possess such organelles (Beakes, 1989; Powell and Blackwell, 1995). Barr and Désaulniers (1987) could not clearly match the zoospore of *Lagen* to either the primary or secondary types of zoospores found among Oomycetes (cf. possible evolution of oomycete zoospore types, Blackwell and Powell, 2000). Barr and Désaulniers (1987) did not consider such an attempted categorization as necessarily meaningful for organisms such as *Lagen*, which produce only one form of zoospore. In a later publication, Barr and Désaulniers (1990), based on various life cycle features, seemed certain that *Lagen* should be placed in the Oomycetes; beyond that, as mentioned, they merely postulated a lagenidialean connection for *Lagen*, indicating that “its phylogenetic relationship to other Oomycetes remains unclear.” Dick (2001) likewise was unable to determine precise relationships for *Lagen*, concluding that it was possibly distinct among Peronosporomycetes (Oomycetes), and basing a new family, Lagenaceae (*incertae sedis*), upon it. Within Oomycetes the relationships of *Lagen* remain uncertain, a circumstance pertaining as well to a number of other holocarpic oomycete genera (see, for example, Blackwell, 2010). Systematic clarification will no doubt occur if molecular sequences for such organisms become available.

QUESTIONS OF GENERIC NOMENCLATURE

Given (1) the detailed generic description of *Lagen* by Vanterpool and Ledingham (1930), (2) no real confusion with other oomycete genera, (3) an initial inclusion of only a single species (*L. radicola*), and (4) no obviously included additional species, it might be assumed that there would be little problem with the nomenclature of *Lagen*. However, a competing generic name, *Lagenocystis* Copeland (1956), was evident in my investigation. *Index Fungorum* indicated *Lagenocystis* as the current generic name for *L. radicola*; whereas, *Index Nominum Genericorum* listed *Lagen* as correct. Most authors (e.g., Sparrow, 1960; Macfarlane, 1970; Karling, 1981) have used the name *Lagen*, but others (e.g., Dick, 1971, not 2001) employed *Lagenocystis*. Seymour and Johnson (1973) made reference to *Lagen*, but observed that Copeland (1956) renamed this organism *Lagenocystis*—a *nomen novum* (cf. ICBN, 2006, Article 7.3) for

Lagen Vanterpool & Ledingham (1930). Copeland (1956) provided this replacement name (*Lagenocystis*)—for *Lagen* Vanterpool & Ledingham (1930)—because of the existence of *Lagen* Parker & Jones (1859), a putative earlier homonym (for a different kind of organism).

Since *Lagen* Vanterpool & Ledingham (1930) is not a conserved name (ICBN, 2006), it might at first appear that Copeland (1956) was correct in assigning priority to *Lagen* Parker & Jones (1859), and renaming *Lagen* Vanterpool & Ledingham, as *Lagenocystis*. However, Copeland's action missed the mark on two points. First, in "*Lagen* Parker & Jones," Copeland was referencing the name of a genus of Foraminifera (treated nomenclaturally as an animal). Since the botanical code of nomenclature (ICBN, cf. Principle I) is essentially independent of the zoological code, it is permissible for a plant (or fungus, or oomycete) to bear the same name as an animal. There are a number of instances of this, e.g., *Pieris*, the name of member of the plant family Ericaceae, and of a butterfly. Second, Copeland was incorrect in citing Parker and Jones (1859) as the original source of the name *Lagen* (Foraminifera); this foraminiferan name was first established by Walker and Jacob (1798)—see Cushman (1940), and Loeblich and Tappan (1988). The proper origin of the foraminiferan name, *Lagen*, i.e., by Walker and Jacob (1798), is noted in *Index Nominum Genericorum*. In partial defense of Copeland (1956), it can be mentioned that Parker and Jones (1859) were instrumental in establishing a type for the foraminiferan name *Lagen* (cf. Patterson and Richardson, 1988). In any event, *Lagen* Vanterpool & Ledingham (1930) may be used as the generic name for the oomycete root parasite, regardless of use of *Lagen* as an animal name; there is no need for conservation, or for a substitute name. The name *Lagenocystis* Copeland (1956) should be regarded as superfluous (ICBN, Article 52), and a synonym of *Lagen* Vanterpool & Ledingham (1930), cf. Karling (1981). As it turns out, *Lagenocystis* is also the name of an animal (presumed genus of digenetic trematodes) and of an oomycete—use as an animal name (Yamaguti, 1970) coming after the "fungal" usage.

ADDITIONAL HOSTS, POSSIBLE ADDITIONAL TAXA

In addition to wheat, *Triticum aestivum*; rye, *Secale cereale*; barley, *Hordeum vulgare*; and relatives (e.g., *Agropyron* sp.), other hosts for *Lagena radiculicola* have been reported. Truscott (1933) noted finding this parasite in maize and “a number of...wild grasses.” Initially, Vanterpool and Ledingham (1930) had reported occasional attack of finer roots of *Zea mays* under experimental conditions. Macfarlane (1970) noted finding *L. radiculicola* in *Nicotiana debneyi*, and successful inoculation of the parasite in tobacco and cabbage (but not tomato). Macfarlane referred to the finding of an unidentified organism resembling *L. radiculicola* in roots of sugar cane, in Mauritius, by Antoine and Ricaud (1966)—suggesting range extension of this parasite into tropical environments, and raising questions as to host specificity. Karling (1981) mentioned sugar cane (re: the Mauritius “fungus”), along with corn, as a potential host for *L. radiculicola*.

No additional taxa have been added with certainty to *Lagena*; *L. radiculicola* is still the only generally accepted species. Nonetheless, other possible taxa have been mentioned. Truscott (1933) wondered if branched-thallus individuals (Fig. 2) of *L. radiculicola* might be a taxon distinct from simple, sac-like thallus specimens (Fig. 1), but seemed to dismiss this idea after observing intergrading forms. Sparrow (1939) described a one-celled, saccate, sometimes lobed parasite of eggs and embryos of rotifers, that he named *Lagenidium oophilum*. Sparrow discussed the similarity of the thallus of this rotifer parasite to that of the parasite of wheat roots, *Lagena radiculicola*. Although Sparrow described his organism (including Latin diagnosis) as a species of *Lagenidium*, he suggested that it could eventually be placed in *Lagena*, and, if so, that the name would be *Lagena oophila*. Sparrow thus, intentionally or not, introduced the binomial, *Lagena oophila*. Sparrow (1960), though, continued to recognize this rotifer parasite as a species of *Lagenidium*, as did Karling (1981). The eventual disposition of Sparrow's *Lagenidium oophilum* remains in question. Dick (1997) included this species under *Myzocytiopsis* as a “doubtful” taxon. *Myzocytiopsis* was established (Dick, 1997) for *Lagenidium*- or *Myzocytiopsis*-like organisms, with intrasporangial zoosporogenesis, which are parasites of animals (rotifers, aschelminths)—see Pereira and Vélez (2004). Dick (2001) continued to list *M. oophila* (Sparrow) Dick

as a doubtful species of *Myzocytiopsis*. It at least seems clear from the foregoing that *Lagenidium oophilum* Sparrow (1939) has not been accepted as a member of the genus *Lagena*. Seymour and Johnson (1973) described a somewhat similar, unnamed rotifer-egg parasite they likened in some ways to *Lagena radiculicola*; however, zoosporogenesis of their organism is intrasporangial, and there is similarity in other regards as well to *Myzocytiopsis fijiensis* (cf. Seymour and Johnson, 1973; Dick, 1997). Without molecular sequence data, however, any such relationships are difficult to decipher with certainty.

As for other possible taxa of *Lagena*, Dick (1971) briefly discussed an unnamed organism parasitizing the water mold, *Aphanomyces*. He described this parasite as “holocarpic” and “polyoosporous,” with a “reserve globule disposition similar to *Lagenocystis* [*Lagena*] and the eccentric *Achlya* species.” In an earlier reference Dick (1970) noted that oogonia of the *Aphanomyces* invader “contained several apparently eccentric oospores”—suggestive of *Lagena* oospores illustrated by Macfarlane (1970). The *Aphanomyces* parasite, however, was not illustrated, nor was information provided on its thallus morphology or zoospores. Hence, information is too sketchy to assess its taxonomic identity. It was not mentioned in Dick (2001).

A final organism to discuss is associated with leaf-spot disease of *Panicum repens* in India. This grass could be found in dry conditions at certain times of the year and semi-aquatic conditions at others, depending on rainfall. The infecting “fungus” proved to be an oomycete, described as *Petersenia panicicola* by Thirumalachar and Lacy (1951). The genus *Petersenia* was established by Sparrow (1934) for *Olpidiopsis*-like organisms with lobed thalli, parasitic in certain marine algae, or water-molds (see also Sparrow, 1960). The existence of a “terrestrial” *Petersenia* was unusual, and Thirumalachar and Lacy (1951) thought the thickened “resting sporangia” of *P. panicicola* to represent a land-existence adaptation. Perhaps in consideration of its generally terrestrial habitat, Dick (2001) listed *P. panicicola* (as a “doubtful” but not excluded species) under *Lagena*. Under *Petersenia*, Dick (2001) listed *P. panicicola* as “excluded” and “possibly related to *Lagena*.” Information and illustrations in Thirumalachar and Lacy (1951) and Karling (1981), though, would lead one to question Dick’s tentative placement in *Lagena*. Sporangia of *Petersenia panicicola* are

often deeply and irregularly to more or less regularly lobed, the persistent lobing in some cases being almost “stellate” in appearance. Although there is variation in thallus/sporangial lobing of *Lagena radicola*, it does not attain the strikingly and firmly lobed appearance of *Petersenia panicicola*. Also, zoosporogenesis in *Petersenia panicicola* is apparently intrasporangial (based on sparse information in Thirumalachar and Lacy), not extrasporangial and vesicular (as in *Lagena*). Thus, *P. panicicola* seems better placed morphologically in *Petersenia* than in *Lagena*; it is, in fact, recognized under *Petersenia* in *Index Fungorum*. *Lagena* should for now remain monotypic.

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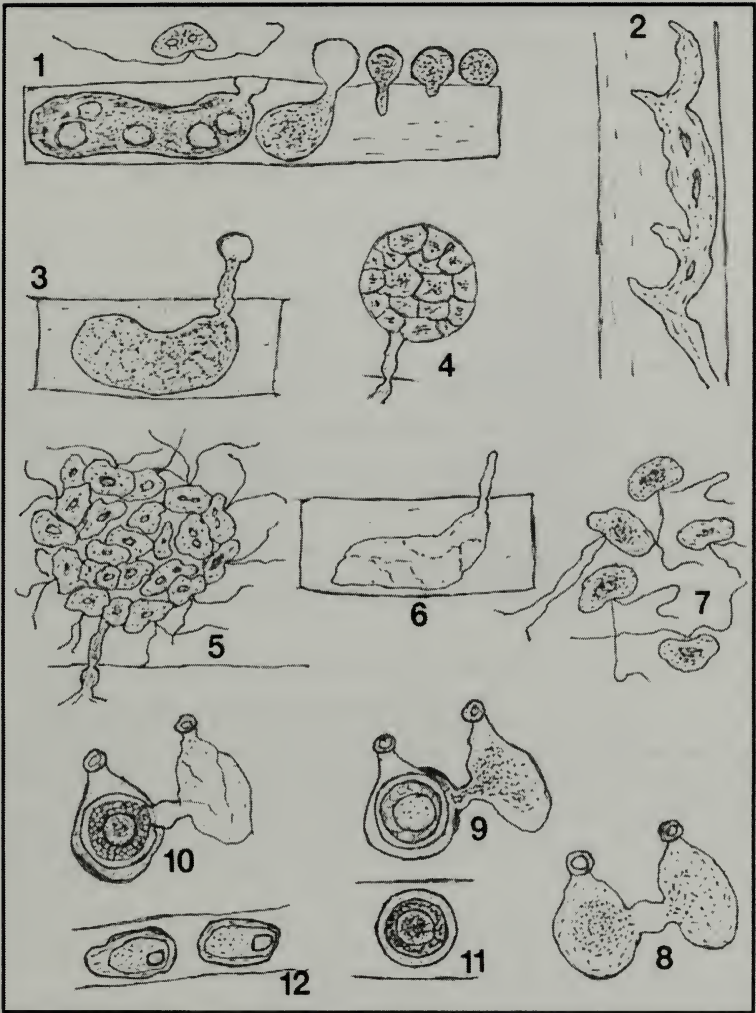
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Figs. 1-12: *Lagena radiculicola* (infecting wheat and barley). Fig. 1: Sac-like thallus developed from encysted zoospore; neck and collar area of thallus are attached to the host cell. Fig. 2: Branched thallus. Fig. 3: Sporangium; discharge tube forms from neck area. Fig. 4: Zoospores cleaved in vesicle at tip of discharge tube. Fig. 5: Mass of zoospores. Fig. 6: Empty sporangium after discharge. Fig. 7: Free-swimming, biflagellate zoospores. Fig. 8: Gametangia with conjugation tube. Fig. 9: Contents of male gametangium flowing toward oosphere in female gametangium. Fig. 10: Oospore developing, post fertilization. Fig. 11: Mature, centric oospore. Fig. 12: Eccentric form of oospore. Figs. 1,3,4,5,6,7,8,9,10,11 after Vanterpool and Ledingham, 1930; Fig. 2 after Truscott, 1933; Fig. 12 after Macfarlane, 1970.



Figures 1-12. See caption of previous page.